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ELECTRICAL RESPONSES TO PHOTIC STIMULATION IN THE EYES AND NERVOUS SYSTEM OF NEREID POLYCHAETES[1]

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The responses of a variety of polychaetes to photic stimulation have been examined by several investigators taking advantage of rather clear-cut, often stereotyped behavior patterns influenced by light. Perhaps the easiest to deal with is the withdrawal reflex on sudden increases and/or decreases in light level characteristic of many tubiculous forms (Nicol, 1950). More complex behavior patterns have been subjected to analysis as in the work of Herter (1926) and Ameln (1930) who studied the behavior of *Nereis diversicolor* under varying conditions of light. With the aid of prostomial eye ablation, they attempted to ascertain the possible differences in the function of the anterior and posterior pairs of prostomial eyes.

Clark (1956), utilizing some species-specific variability in the photoreceptors of *Nephtys*, studied the influence of light on locomotion and orientation in members of that genus. After a consideration of the role of the supra-esophageal ganglion-associated photoreceptors, the suggestion that pigment-surrounded undifferentiated dermal cells may play a part in photo-reception was put forth on the basis of apparent photosensitivity in the posterior part of the worm.

Hauenschild (1961) demonstrated that prostomial eyes are not necessary for the light-controlled triggering of metamorphosis to the heteronereid stage in *Platynereis dumerilii*. Evans (1965) has shown that the withdrawal response to shading is not dependent on the presence of prostomial eyes and the supraesophageal ganglion in *Nereis diversicolor*. Such results make it clear that structures other than prostomial eyes function in photo-reception. These may be unspecialized dermal cells as suggested by Clark (1956), specialized dermal photoreceptors, or photosensitive neurons in the central nervous system. There is ample precedent for neuronal photosensitivity in invertebrates, (Welsh, 1934; Prosser, 1934b; Arvanitaki and Chalazonitis, 1949; Kennedy, 1958, 1960; Yoshida and Millott, 1959) and there is no *a priori* reason to rule it out in polychaetes.

Cells that are presumed to be photoreceptors are known in oligochaetes (Hess, 1925). Similarly constructed cells are known to function in light perception in Hirudinea, (Mann, 1962, for summary; Hansen, 1962; Walther, 1966; Clark, 1966) and are the only obvious photoreceptor equipment in a few polychaetes (*e.g., Nephtys,* Clark, 1956; *Polyophthalmus,* Hesse, 1899). Such cells have not been noted in nereids, although Langdon (1900) described rather complex "spiral organs" she thought to be photoreceptors in *N. virens*. Smith (1957), however, failed to confirm their existence in the species of nereids he studied. None of the simple sensory cells described by him are obvious photo-receptors.

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Work on the electrophysiology of polychaete annelids has been mostly concerned with the functioning of the giant fiber systems (Bullock, 1945, 1948; Nicol and Whitteridge, 1955; Horridge, 1959; Hagiwara, Morita, and Naka, 1964), although aspects of the control of locomotion in *Nereis* (Wilson, 1960), the functioning of mechanoreceptors in *Nereis* and *Harmothoë* (Horridge, 1959, 1963), and the response to mechanical stimulation in *Branchiomma* (Krasne, 1965) have been reported. To date there has been no report of an electrophysiological analysis of any aspect of photoreception in a polychaete, and very few such studies in any annelid (*e.g.*, Prosser, 1934a, 1935; Walther, 1966).

The present report is primarily concerned with the shadow reflex in *Nereis diversicolor* and *Platynereis dumerilii* and the possible role of the dermal and prostomial photoreceptors. Observations on other species are included, where pertinent, for comparison.

A preliminary report of some of the results of this study has appeared elsewhere (Clark, 1966).

Materials and Methods

Specimens of *Nereis diversicolor* and *Platynereis dumerilii* were the principal experimental animals, but preparations of *Nereis virens* have also been examined. *N. diversicolor* was collected as required from the banks of the Avon near Bristol. Animals were stored in aerated 50–70% sea water at room temperature or in a refrigerator at 2–4°C. In both cases the worms were provided with glass tubes of a suitable diameter to permit irrigation. Worms handled this way appeared healthy and responsive for at least one week and frequently much longer. *N. virens* was collected at Clevedon on the Bristol Channel and used shortly after collection. Specimens of *P. dumerilii* were supplied by the Marine Station, Millport, and were used within a few days of delivery.

Electrical recording was accomplished in a variety of ways. Electroretinagrams (ERGs) were initially recorded with electrolytically polished stainless steel needles, insulated to the tip, by simply thrusting the electrode through the cuticular lens into the "pupil." This procedure, however, resulted in considerable damage and preparations of this sort did not last more than about one hour. Consequently, most of the ERGs were recorded with glass micropipettes filled with 3 *M* KCl (5–10 megohms resistance in KCl) thrust into the back of the eye after ventral exposure of the supraesophageal ganglion and eyes. Such preparations gave good responses for up to four hours. The amplifier used for the electroretinagrams was a neutralized input capacity amplifier (Bioelectric Instruments, Inc., Type DS2C). Records from the ventral nerve cord, circumesophageal connectives, and segmental nerves were taken either with the previously described steel electrodes or with platinum-irridium hook electrodes. In both cases a Grass P-5 A. C. pre-amplifier was used, with a high impedance input device (Grass, HIP-5) for the steel electrodes. In all cases the results were displayed on a Tektronix Type 502 dual beam oscilloscope and photographed with a Grass C-4 kymograph camera.

The light source consisted of a 6 V, 48 W tungsten filament microscope lamp (Cooke, York) operated from the 6 V laboratory D. C. supply. A shutter was fitted to this which permitted giving light flashes of 1 to 0.01 second duration and could be operated "bulb" or "time" for longer duration flashes. A selenium self-

generating photocell intercepted a portion of the beam so that stimulus duration could be monitored on the second beam of the oscilloscope. The lamp housing had provision for introducing filters and a Chance type ON 22 heat filter was kept in place at all times. This prevented any significant temperature rise over the 1–3 hours of the experiments once the preparation had reached room temperature (15–20° C). In no case did the temperature of the bathing medium rise above 20° C, and most experiments were done at 15–17° C.

Light intensity was controlled with neutral density filters (Kodak) and are expressed in terms of per cent transmission of unit intensity (heat filter only) which was approximately 1000 foot candles at the surface of the bathing medium (measured with an S. E. I. Exposure Photometer).

No attempt was made to localize the stimulus to the structure under investigation. This was accomplished in most cases by surgical isolation, and the types of preparations used are described in the text. Anesthesia was not used because recovery failure was a common experience with this material.

Because of the extreme sensitivity of the preparations to mechanical perturbations, it was necessary to "shock mount" the photographic shutter used and to intersperse control shutter operations during the experiments. This was done by operating the shutter and performing all other manipulations with the light source turned off. Such controls always followed the same time course as the experimental procedures. If the preparation responded to shutter vibrations at any time, the run was discontinued until the situation was corrected, and all data previous to the spurious response were discarded.

The medium bathing preparations consisted of 50% sea water in the case of *N. diversicolor* and full strength sea water for the other preparations. This value is well above the point at which *N. diversicolor* from a variety of habitats begins to regulate chloride (Smith, 1955), but information on the regulation of other ions at this salinity level is not available.

Preparations were kept in the dark for at least ten minutes between light flashes unless shorter or longer intervals were appropriate to the response being tested. These other intervals will be apparent in the context of any particular observation.

Results

Responses of the prostomial eyes

An electrode introduced either through the cornea or into the ventral surface of the prostomial eye records an extracellular response to a light flash that is illustrated in Figure 1. This consists of a relatively fast negative-going potential (with respect to an indifferent electrode in the bathing medium), followed by a brief positive deflection, and a slow decay to base line (Fig. 1, A, B). If the preparation is dark adapted for more than 15 minutes, the transient is followed by a "steady-state" potential that is maintained in the light until "off" (Fig. 1C, D). The graded nature of the ERG at different light intensities is shown in Figure 1. If one follows the interpretations of Ruck (1961) of the ERG of the insect ocellus, then the negative components are said to originate in the photoreceptor cell rhabdomere membrane, the positive component in the receptor cell axons. The waveform is thus similar to that seen in a number of arthropod eyes with the exception that spikes are not recorded at this level as they frequently are in arthropod eyes.

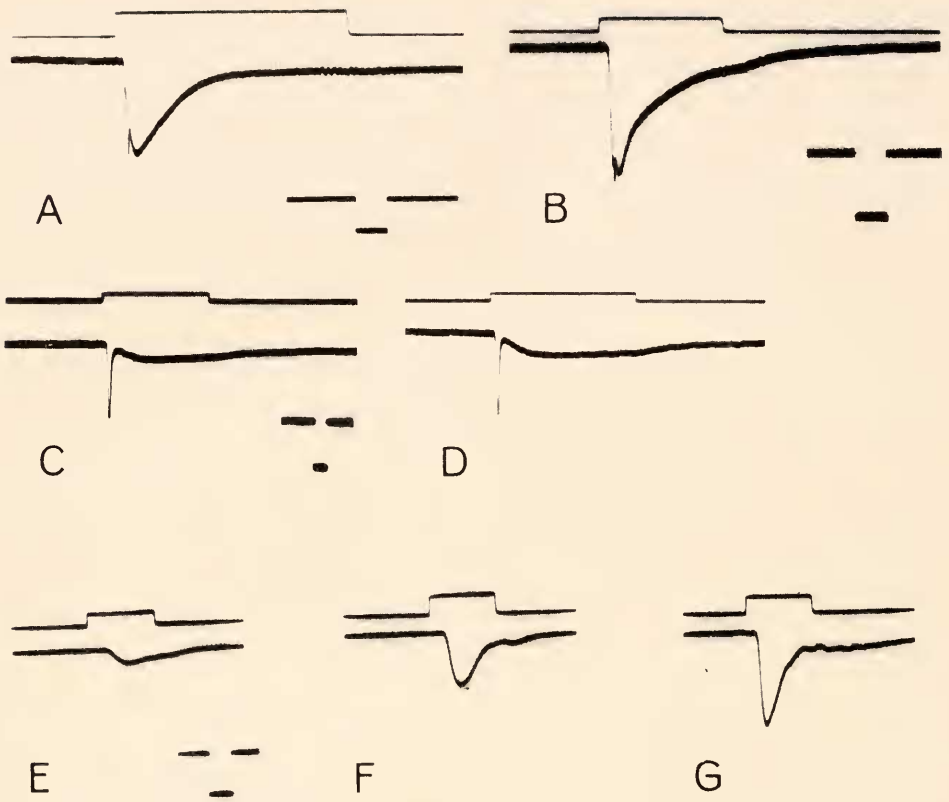

FIGURE 1. Electroretinagrams from nereid polychaetes. A. and B: Anterior eye of *Nereis diversicolor*. Calibration, 1 mV, 20 ms. C: Posterior eye of *Platynereis dumerilii*. D. Anterior eye of *P. dumerilii*. Calibration for both C and D, 1 mV, 400 ms. E through G: Posterior eye of *P. dumerilii* showing graded response to increasing light intensity; intensity in E = 1% of unit intensity, in F = 10%, in G = 100%. Calibration, 2 mV, 200 ms. In all traces, upward deflection of upper beam indicates "on," downward deflection of lower beam indicates negativity of active electrode. All recordings D. C.

None of the information I have obtained indicates any major consistent difference between *N. diversicolor* and *P. dumerilii* nor between anterior and posterior eyes of the two species.

Attempts to follow the course of dark adaptation were plagued by movement of the preparation, but were finally moderately successful. This could only be judged by a return to a dark-adapted criterion amplitude following a period of light adaptation. If the return to initial amplitude increased with time in the dark, the experiment was judged successful. Using this as a criterion, dark adaptation is approximately two-thirds complete in fifteen minutes, but not complete for ninety minutes or more. Again, no marked difference was noted between species or pairs of eyes. No attempt to vary light intensity or period of light adaptation was made.

There is thus no evidence that any behavioral differences said to be mediated by anterior or posterior pairs of eyes (Herter, 1926; Ameln, 1930) can be ascribed

to differences in the properties of the photoreceptors themselves. Such differences are almost certainly centrally mediated, but the rather crude information presented here does not necessarily rule out the possibility that there are differences in the eyes other than the obvious positional ones.

Responses recorded from the nervous system.

A. Supra-esophageal ganglion It is possible to record an inverted (positive-going) "electroretinagram" from the supra-esophageal ganglion. Destruction of the eyes abolishes this response, so it is assumed to originate in the prostomial eyes.

Using steel electrodes, spike potentials have been detected in the brain at "off," but records are so inconsistent that it is impossible to assign them to eyes or possible prostomial dermal photoreceptors.

B. Circumesophageal connectives Records taken with external hook electrodes from the circumesophageal connectives show no activity clearly associated with "off"

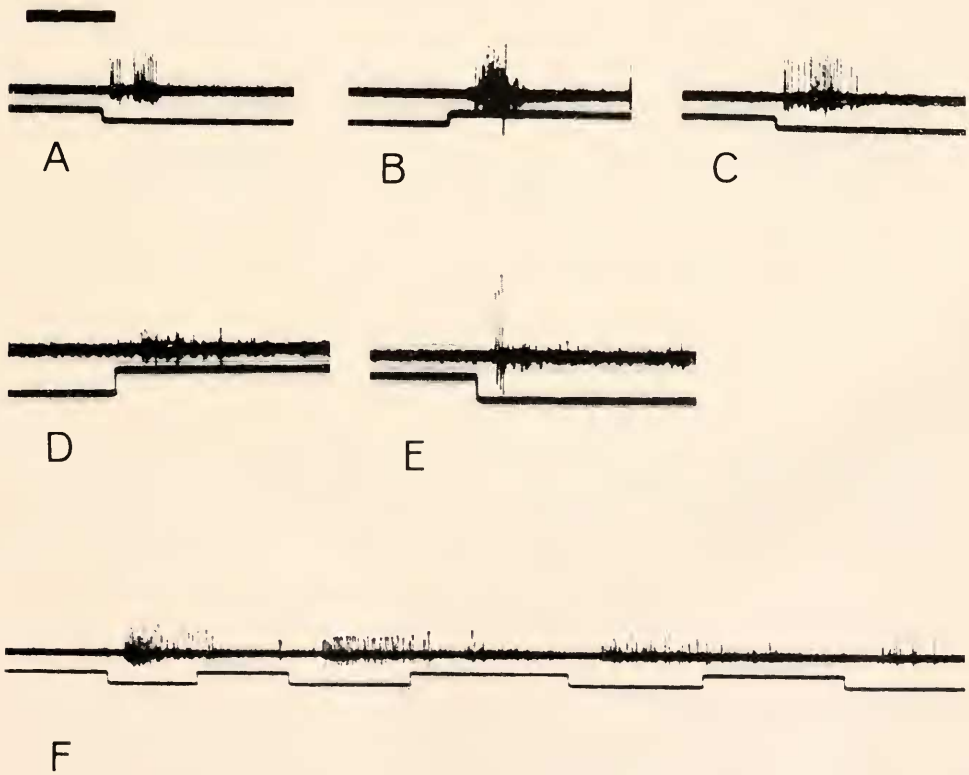

FIGURE 2. Recordings taken with steel electrodes from the ventral nerve cord of *N. diversicolor*. A–C: sub-esophageal ganglion. D: "on" response from cord posterior to sub-esophageal ganglion in a headless *N. diversicolor*. E: "off" response in the same preparation. F: recording posterior to a cut in the ventral nerve cord in the posterior half of *N. diversicolor*. Time calibration in A = 500 ms and applies to all records.

or "on." On a few occasions the impression was gained that slow build up in activity followed "on," but there was so much "spontaneous" activity that was so variable it was impossible to make a clear association. On the other hand, large fiber activity was easily demonstrable by mechanical stimulation of the prostomial antennae indicating at least some functional pathways. On a few occasions, bursts of activity at "off" were detected by steel electrodes thrust into the circumesophageal connective, but large external electrodes failed to detect this.

These results indicate that the two kinds of information are transmitted over different pathways to the ventral nerve cord where both activate the giant fibers. This would also seem to provide some evidence that different giant fibers may be activated by the different sensory modalities. The circumesophageal activity recorded on mechanical stimulation is clearly giant fiber activity and as the lateral giant fibers are the only ones found in the circumesophageal connective (Nicol, 1948; Smith, 1957), it is almost certainly this that is recorded. As the median giant fiber is also activated by anterior stimulation there are either separate fibers serving as input to the median fiber (terminating in the sub-esophageal ganglion) or there is cross-over between the two. Since the lateral giants have the higher threshold to mechanical stimulation (Bullock, 1945), the system consists of either separate pathways or a synapse to the lateral giants that requires spatial and/or temporal summation. In any event, it seems clear that the anterior terminations of the lateral giant fibers are not activated via the anterior photoreceptors.

C. Subesophageal ganglion If the head and circumesophageal connectives are left intact and the ventral nerve cord posterior to the subesophageal ganglion is intact, the activity reproduced in Figure 2A, B, may be recorded from the subesophageal ganglion. There is a burst of fine fiber activity at both "off" and "on." Severing the ventral nerve cord just posterior to the subesophageal ganglion does not appreciably affect this activity (Fig. 2C). Under these circumstances there is still no indication of giant fiber activity, but it does show that photic information is transmitted from the anterior part of the worm, presumably via the circumesophageal connectives, but possibly also from other sensory input, directly to the subesophageal ganglion. The difference in latency between the "off" and "on" responses may simply be due to different transmission velocities in the internuncial fibers responding to the two conditions.

D. Ventral nerve cord If records are taken from any point in the ventral nerve cord there is almost always a fine-fiber response at "on" (Fig. 2D), and, if the animal has been left in the light for more than 30 seconds, a giant fiber response at "off" *if the anterior part of the worm is included in the preparation* (Fig. 2E). If the nerve cord is severed at any point posterior to about the middle of the worm and the recording taken from posterior to the cut, there are both "on" and "off" responses, but these are fine fiber responses. Transferring the electrode anterior to the cut records giant fiber activity at "off" in the same worm. That the giant fibers (paramedials) activated by posterior afferents are still functional and the electrode will record their activity is easily demonstrated by mechanical stimulation of the posterior end of the worm. This indicates that photoreceptor input to the giant fiber system is limited to, at most, the anterior half of the worm, but also that photoreceptors are present posteriorly that activate only the fine fiber system (Fig. 2F).

If the head (prostomium) of the worm, or, indeed, the first several segments are removed, the same cord responses are obtained, proving that the prostomial eyes are not necessary for the giant fiber response. The only difference consistently apparent in the cord responses of intact and headless worms is an increase in latency of the giant fiber response (recording from the same site in the same worm) in the headless animals (Fig. 3A and B). Three explanations for this phenomenon seem possible. 1. The giant fiber response is normally triggered by the eyes which

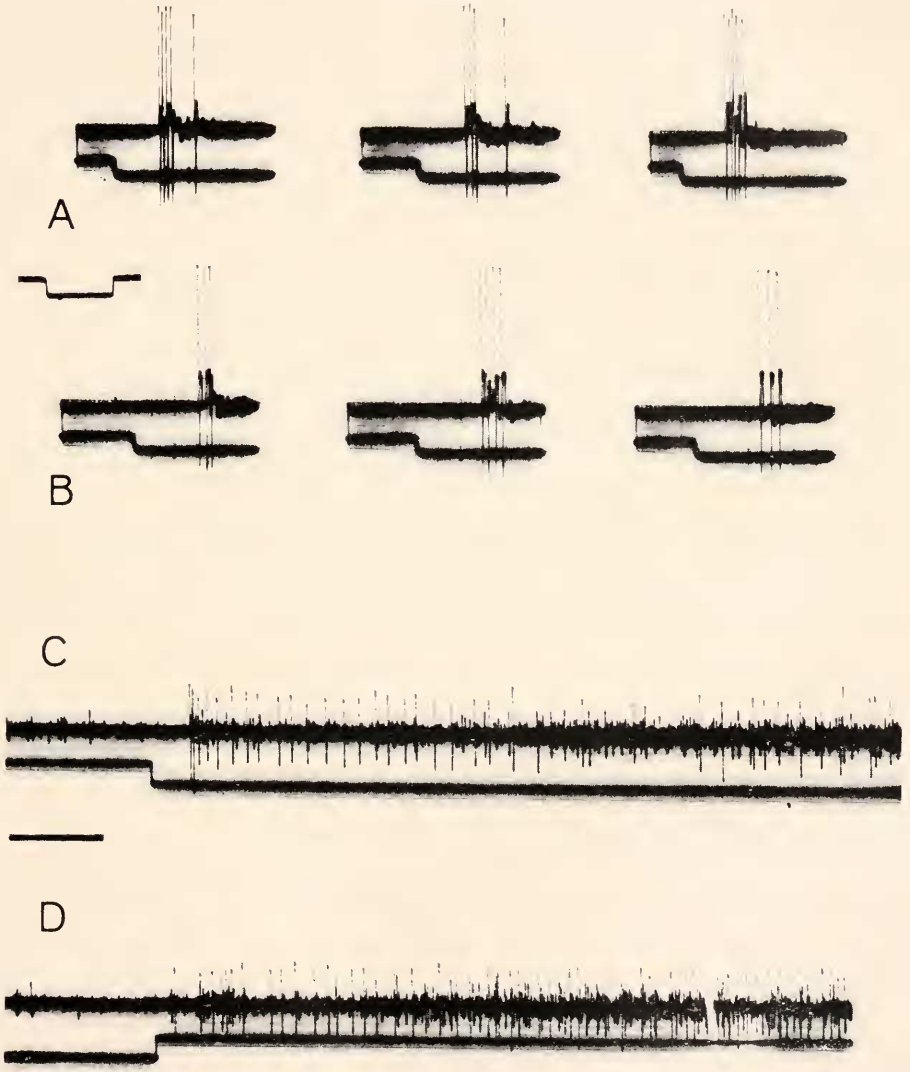

FIGURE 3. A, B: records taken from the same location on the ventral nerve cord in the same preparation of *N. diversicolor*. A, with head intact; B, headless. Time calibration = 150 ms. C: "off" response in segmental Nerve II, *N. virens*. D: "on" response in the same preparation. Time calibration = 500 ms.

have a more direct connection to the giant fiber system and hence a shorter latency; 2. The response is due to temporal and/or spatial summation of the dermal photoreceptor input and removal of the head removes many dermal photoreceptors leaving more scattered, less directly-connected receptors to serve as the trigger; or, 3. it is an injury effect. The last explanation could not be definitely ruled out, but the longer latency persisted unchanged for at least an hour after head removal.

Another aspect of the giant fiber response should be mentioned. In many of the records it is clear that more than one type of giant is firing, and in some only one type, but repetitively. If shadows are delivered in succession, the first few will show multiple firing, but the record soon shows activity from a single giant fiber, always the smaller if two amplitudes were previously apparent. A possible interpretation of this observation is that a shadow causes one or a series of spikes in the median giant fiber. This in turn triggers a contraction, and as soon as the worm begins to move there is ample input from, *e.g.,* bristle receptors to trigger more median spikes and at times, the lateral giant fibers. Consequently, as long as there is movement in the worm the sensory input is not restricted to that from the photoreceptors.

E. Localization of dermal photoreceptors It was first established on several specimens that the nerve cord itself was not photosensitive to the extent that it gave any of the responses noted above. Isolated nerve cords showing good spontaneous activity and nerve cords *in situ* but with all segmental nerves cut showed no change in activity at "on" or "off." However, as long as there was some connection via segmental nerves to the anterior body wall and parapodia, a giant fiber response could be obtained at "off." The smallest fragment actually recorded from that gave this response was made up of seven segments.

Parapodial removal in headless (prostomium and peristomium removed) worms abolished the response, but if the head was intact the giant fiber response always occurred, even with the parapodia removed. Dorsal body wall removal alone did not abolish the response. From this it was concluded that the dermal photoreceptors are widely distributed on the prostomium and the peristomium, and the parapodia. They may be present on the dorsum, but it is certain that they are not limited to that region. The fact that parapodial removal abolished the response in headless worms may also be taken to prove that the photoreceptors are not located ventrally, for parapodial removal would not disrupt ventral sensory input. I have not attempted to localize the receptors more precisely by removing bits of the parapodia in turn, but the possibility that they are limited to, *e.g.,* cirri, exists. In connection with these ablation experiments, the "spiral organs" described by Langdon (1900), have the following distribution: outer and lateral surfaces of the palp bases; outer surfaces of bases of cephalic cirri; dorsal surface of the prostomium; the first setiger on both the dorsal and ventral surfaces. The number located mid-dorsally decreases posteriorly. They are also found on the tips of the gill lobes of each parapodium. In general, the number is related to body diameter and so decreases posteriorly. This distribution fits fairly well with the observed activity, but the fact that these complex organs have not been seen by other workers (*e.g.,* Smith, 1957) casts doubt on the possible causal relationship. There is no other single type of sensory structure (*i.e.,* different from the others) that has been described to have a distribution that would explain the results.

F. Segmental nerves If the body dermal photoreceptors are located principally on the parapodia (as the evidence indicates) one would expect to be able to record sensory input in segmental Nerve II in response to light stimuli. Attempts to record this activity have been unsuccessful despite considerable effort. I have been able to record sensory input from a variety of mechanoreceptors, but there is no discernible response to light or shadows. Horridge (1963) has shown that peripheral sensory convergence is unlikely by demonstrating that Nerve II has a few large axons identified as mechanoreceptor afferents and a few thousand small ones. This makes it possible to surmise that the photoreceptor axons are small and thus difficult to record from in a nerve bundle that is dominated by the mechanoreceptor response.

Records from the central stumps of Nerve II in *N. virens* show bursts of activity at "off" and at "on" (Fig. 3C, D). This is also true of Nerves I and IV, although I have obtained very few records from the latter two. I have not succeeded in recording any activity from Nerve III. Records from Nerve II in *N. diversicolor* are similar to those shown for *N. virens*. The long persistence of activity in Nerve II does not correspond to cord activity where the responses to light and shadow are relatively brief. The continued activity may be due to the stimulation of movement in the preparation. The fact that the response in the parapodial nerve occurs at both "off" and "on" in *N. diversicolor* indicates that it is not due to the giant fibers, for they do not fire at "on" in that species. Further evidence of this is seen in the parapodial "pointing" reflex. If *N. diversicolor* is mechanically stimulated anteriorly, the worm withdraws its head and all of the parapodia are swung in toward the body pointing forward. If the tail is stimulated, it is withdrawn and the parapodia point backward. If the light intensity is lowered (shadow) the forward pointing reflex is evoked; if the light intensity is increased, the backward pointing reflex follows. The latter condition does not generate giant fiber activity, but can still lead to the useful response of tail withdrawal.

G. Habituation Several reports on habituation to stimuli in nereid polychaetes have appeared (Clark, 1960a, b; Evans, 1965; Evans, 1969a, b; Clark, 1966 for summary). These reports establish that the habituation process seen at the behavioral level is not a simple one. It appears that habituation to any one narrowly defined stimulus is straight-forward, but if two kinds of stimuli are interspersed, or if there is some slight change in the way a stimulus is presented, the time course of the process may be altered, and in some cases the response enhanced (Clark, 1960b, 1966).

In this study, the number of trials to failure of the giant fiber system was many fewer than that of the fine fiber response. If the light was turned off every thirty seconds for 2–3 seconds the giant fiber response failed after a maximum of 25 trials. If the intertrial period was reduced to 5 seconds, the giant fibers failed after 1–4 trials. In both cases fine fiber responses continued for as many as 56 trials with 30 second intervals and 20 trials at 5 second intervals. In neither case were fine fiber responses taken to extinction.

In the behavioral work it was impractical to make a distinction between fast and slow withdrawal after the first few responses, but a difference between head and tail withdrawal has been observed. Tail withdrawal is slower than head withdrawal, and the former occurs at light "on," the latter at light "off" (Evans,

1969a). One cannot say the fine fiber activity generates tail withdrawal and giant fiber activity head withdrawal in any general sense, but in the response to photic stimulation one can say that any known response involving the giant fibers is always correlated with head withdrawal. The fine fiber response, on the other hand, is not necessarily correlated only with tail withdrawal.

The fact that fine fiber responses persist after the giant fiber response is extinguished indicates that the site of habituation for the latter is at some point on the sensory side, perhaps at the sensory-to-giant synapse. Failure of the worm to respond after less than 40 trials (Evans, 1969a) indicates that a second point of failure is on the motor side of the central nervous system because the fine fiber central activity persists beyond this point.

Attempts to demonstrate re-sensitization of the giant fiber response by applying a mechanical stimulus after giant fiber failure were unsuccessful.

Discussion

The results of this study provide no evidence for any difference in the two pairs of prostomial eyes as far as the sensory event is concerned. Any behavior difference that might be ascribed to one pair or the other is probably due to central processing or to the position of the eyes. The anterior eyes are directed forward and up, the posterior pair laterally and up, and it is thus quite likely that they are stimulated differently.

The wave-form of the electroretinagrams presented are not markedly different from those seen in, *e.g.*, insect ocelli recorded under similar conditions. Spikes are not seen, however, and this may indicate that the photoreceptor cells themselves do not spike, but certainly does not prove it. Intracellular recording may be expected to yield good evidence on this point, but that has not been possible with this material.

The brief positive "notch" on the leading edge of the ERG (Fig. 1A, B) may be due to the passive spread of an axonal event as Ruck (1961) has suggested for insect ocelli, but it may be indicative of a regenerative event such as that seen in *Limulus* retinular cells (Benolken, 1961; Benolken and Russell, 1966). Again, however, intracellular recording is required for substantiation of this.

The ventral nerve cord responses offer satisfying electrical correlates to some aspects of known behavior, present some puzzles, and uncover new information not readily obtainable with behavioral techniques. Most of this information can be applied only to *N. diversicolor* with confidence.

Fast head withdrawal and the forward-pointing parapodial reflex is associated with a *decrease* in light intensity behaviorally, and this stimulus generates a giant fiber response in the central nervous system. An *increase* in light intensity usually leads to relatively slow tail withdrawal and the backward-pointing parapodial reflex (Evans, 1969a). Under these conditions only a fine fiber response is seen in the cord. Further, if the anterior part of the worm is excluded, giant fiber responses are not seen either at "on" or "off" which suggests that a tail withdrawal response to photic stimulation of the posterior part of the worm is not mediated by the giant fibers. A system of this kind places the emphasis on saving the head which is the structure that is normally out of the burrow during feeding and thus in greatest jeopardy. On those occasions when the tail becomes exposed, the increase in

illumination would be sensed and lead to tail withdrawal. It would also seem that if only the tail was exposed, and for some reason was not retracted into the burrow, a sudden decrease in light intensity would also elicit tail withdrawal. Under the usual laboratory conditions for examining behavior in intact animals this event is seldom seen because the giant fiber response generated in the anterior part of the worm would override the posterior "off" event. The advantage of preserving the head for purely sensory and feeding reasons is obvious, but it is also the case that in *Nereis* heads cannot be regenerated while tails can (Cassanova, 1955).

The evidence that the prostomial eyes alone are capable of generating a giant fiber response is ambiguous. There was no satisfactory way of ablating all possible dermal photoreceptors to test this. It is clear, however, that the prostomial eyes are not necessary for the response. The only apparent effect of eye removal (which in the observations reported involves at least removal of the prostomium as well) is an increase in latency of the giant fiber response. This may indicate the eye contribution, but could just as well be the effect of brain and prostomial dermal photoreceptor removal.

The absence of activity in the segmental nerves associated with light regimen is somewhat puzzling in view of the ablation experiment results. Horridge's (1963) observations of the morphology of the segmental nerves offer the most likely explanation.

The efferent activity in the segmental nerves is about as one might expect for normal motor discharge to the parapodia and body wall muscles. This study does not distinguish between possible different kinds of motor output (slow, fast, inhibitory), nor does it distinguish between motor and efferent sensory activity as described by Horridge (1963). The correlation with the light regimen is satisfying, but not unexpected.

The contribution this study makes in the explanation of habituation is to suggest the possible points of synaptic failure by demonstrating that neural activity persists for a greater number of trials than does behavioral activity. This result is of limited significance because considerable variability is quite likely a characteristic of these events and many more examples are needed to establish the relationship.

The hospitality of the late Professor J. E. Harris (subsequently Vice-Chancellor), Department of Zoology, University of Bristol, is gratefully acknowledged. Professor R. B. and Dr. M. E. Clark were particularly helpful in all phases of the work in England, and in making us feel welcome and ensuring a most enjoyable and profitable sabbatical year. All members of the Zoology Department at Bristol were considerate and friendly, and they have my sincere thanks.

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Summary

1. Anterior and posterior pairs of prostomial eyes in *Nereis diversicolor* and *Platynereis dumerilii* display similar electroretinograms.

2. Electrical responses recorded from the ventral nerve cord elicited by changes in the level of illumination with and without prostomial eyes are as follows: (a) Prostomial eyes alone may be capable of triggering a giant fiber response at "off." (b) Ablation of prostomial eyes leads to a longer latency in the giant fiber response but does not abolish it. (c) In the absence of prostomial eyes a giant fiber response is elicited at "off" only if the light level change involves the anterior part of the worm. (d) Fine fiber responses at both "off" and "on" occur in the absence of prostomial eyes when the change in illumination occurs at any place on the body of the worm.

3. Localization experiments indicate that dermal photoreceptors are located primarily on the pro- and peristomium and on the parapodia.

4. Attempts to habituate the cord responses indicate that the site of habituation for the giant fiber response is on the sensory side of the pathway.

5. The significance of the different responses to illumination changes (fast head withdrawal, slow tail withdrawal) in relation to the mode of life of the worm and its powers of regeneration are discussed.

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